1 **The changing patterns of plant naturalisation in Australia.**

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19

20 *Article type:* Biodiversity Research

21 *Running title:* Plant naturalisation in Australia

22

23 *Word count:* 4,999 (main text and acknowledgements)

24

25 *Number of tables and figures:* 11 *Number of references:* 108

26

27 (A) **ABSTRACT**

28 **Aim** To identify the temporal patterns of plant naturalisation in Australia,
29 particularly the interaction between taxonomy, geographic origin and economic use.

30 **Location** Australia

31 **Methods** From Australia's Virtual Herbarium, we compiled a database of
32 information for the entire naturalised flora of Australia. We then examined the
33 database in discrete time intervals to determine the changes in patterns of
34 naturalised species taxonomy, geographic origin and economic use over time.

35 **Results** Contrary to prevailing hypotheses, we found no evidence to indicate that
36 the rate of alien flora naturalisation is increasing in Australia. The number of
37 naturalised species has grown linearly during the period 1880 – 2000, with the
38 underlying rate of new species detected per thousand specimens declining over the
39 same time period. Despite this, the diversity of both species taxonomy and
40 geographic origin has increased over the last 120 years, leading to increased rates of
41 growth in the total phylogenetic diversity of the Australian flora.

42 **Main Conclusions** By classifying species according to their likely origin and
43 economic use, we are able to infer the circumstances driving the patterns of
44 naturalisation. In particular, we identify how the contribution of individual pathways
45 has changed since European settlement corresponding with the socio-economic
46 development of the continent. Our paper illustrates how the changing nature of
47 'high-risk' pathways is relevant to directing interventions such as biosecurity
48 regulation.

49 **Keywords** alien flora, Australia, globalisation, invasive plants, pathway analysis,
50 weed risk assessment.

(A) **INTRODUCTION**

In an era of unprecedented global transport of both people and products, the exchange of species is equally unprecedented (Dalmazzone, 2000; Ricciardi, 2007; Hulme, 2009). Whilst many species have little detrimental impact in their new 'alien' range, a small number have widespread effects (Williamson & Fitter, 1996; Diez *et al.*, 2009; Pyšek *et al.*, 2012). Some alter ecosystem function and contribute to species extinction (Groves & Willis, 1999; Vilà *et al.*, 2011), and others substantially reduce agricultural productivity, increase input costs (Sinden *et al.*, 2004; Pimentel *et al.*, 2005) and degrade cultural values (Bardsley & Edwards-Jones, 2006; Pfeiffer, 2008; Estévez *et al.*, 2013). Australia's island geography and long separation from Gondwana (McLoughlin, 2001) mean that the exchange of these 'neophytes' (sensu Pyšek *et al.*, 2003) can be directly linked to European settlement since the 18th Century because introduction of species by aboriginal Australians appears to have been rare (Kloot, 1984).

Globalisation can be loosely defined as the enhanced global connectivity arising from rapid transport and communication technology (Amin, 2002; O'Rourke & Williamson, 2002). This connectivity has helped drive, and even physically facilitate, species exchange by making information available to a larger number of people more rapidly than traditional communication (Amin, 2002; Hulme, 2009). The conventional hypothesis follows that as globalisation increases over time, so too does the rate of species naturalisation (Perrings *et al.*, 2005; Meyerson & Mooney, 2007; Hulme, 2009). However, beyond this primary hypothesis, little is known about the influence of globalisation on species naturalisation as most geo-political scale analyses have too few introductions to reliably infer such changes.

National plant censuses and inventories of alien species underpin research on biodiversity exchange (Lavoie *et al.*, 2013; Zenni & Nuñez, 2013; Rejmanek, 2014). Considerable effort has developed floral inventories over the last twenty years, at various geo-political scales (see Vitousek *et al.*, 1997; Pyšek, 1998; Lambdon *et al.*, 2008; Jiang *et al.*, 2011; Lavoie *et al.*, 2012; Richardson & Pysek, 2012). The first *Systematic census of Australian plants* was published in 1882 (von Mueller, 1882), however, it was not until the publication of *The introduced flora of Australia and its weed status* (Randall, 2007) that an inventory of Australia's alien flora was completed.

Notwithstanding the literature reviews of Groves (1986), Michael (1994), Scott (2000), Gallagher and Leishman (2015), no comprehensive analysis of the naturalised flora of Australia has been published. Previous analyses have focussed on temporal (Groves, 1998), geo-political (Everist, 1960; Specht, 1972, 1981; Kloot, 1986, 1987a, c, b; Rozefelds *et al.*, 1999; Phillips *et al.*, 2010b), taxonomic (Lonsdale, 1994; van Klinken *et al.*, 2015) or weed status (Phillips *et al.*, 2010a; Murray & Phillips, 2012) subsets of the Australian flora or specific questions such as introduction purpose (Virtue *et al.*, 2004; Cook & Dias, 2006) or introduction success (Diez *et al.*, 2009).

However, the discrete scales of these analyses limit our ability to combine their findings to identify high-risk introduction pathways for management. As has been demonstrated by the Australian Bureau of Statistics in its analysis of census data (ABS, 2013), combining the modes of demographic factors to identify the overall mode (in their case the average Australian), results in a combination of variables that doesn't exist within the dataset, similar to the outcome of a Simpson's

paradox (Simpson, 1951). In our context, this implies that the simple aggregation of the most likely introduction purposes with the most likely source origins or taxonomy to identify the average invader is likely to result in biased estimates of pathway risk; particularly once the data is split into temporal cohorts.

Here we draw together the first comprehensive analysis of the Australian naturalised flora. Using Australia's Virtual Herbarium (CHAH, 2014b), we compiled a database of historical species information. Following a similar conceptual approach to the analyses of Klotz (1987b), Pyšek *et al.* (2003) and Lambdon (2008) we addressed the questions: (1) What are the patterns of plant naturalisation in Australia?; (2) How have these patterns changed over time?; and (3) How do these changes influence the risk posed by human assisted species exchange? By analysing this large dataset we attempt to identify robust trends and their implications for the targeting of management interventions.

(A) **METHODS**

We used the Australian Plant Census to identify the naturalised flora within Australia's Virtual Herbarium. We then used datasets including the Global Biodiversity Information Facility, The Plant List and World Economic Plants in GRIN to compile a database of information for the naturalised flora. Finally, we split the database into smaller time cohorts to determine the changes in patterns of species taxonomy, geographic distribution and economic use over time.

(B) **Data collection**

The complete database of catalogued flora records held by Australian herbaria was exported from Australia's Virtual Herbarium (AVH) (CHAH, 2014b). Records in this master dataset were filtered to include only correctly georeferenced records of vascular plants (tracheophytes) collected in Australia and identified to at least the rank of species. After filtering, 3,074,544 species records were exported for analysis. Records were then imported into the R software environment for statistical computing and graphics (R Core Team, 2013) where the naturalisation status of each species [AVH processed name] was sourced from the Australian Plant Census (APC) (CHAH, 2014a).

The AVH 'processed name' indicates the currently accepted APC species name for a specimen derived from the original 'supplied name' provided by the holding herbaria. This matching process ensures that each record in AVH is systematically checked for taxonomic issues such as invalidity, synonymy and re-classification therefore ensuring the record reflects the species' current, nationally agreed, taxonomy. All families except the Orchidaceae (which has one naturalised species) have been treated by APC, with extensive updates in 2014 (CHAH, 2014a). APC

follows a similar framework to Blackburn *et al.* (2011), with alien species regarded as 'naturalised' once they form self-sustaining populations. 'Casual' species (those with surviving individuals but not self-sustaining populations) and 'cultivated' species were not considered in this analysis as they have not been uniformly treated by herbaria.

Using the APC naturalisation status, the dataset was then split into three subsets for analysis. The first subset, hereafter referred to as the 'native' species, contained 2,737,139 records of 20,376 species not considered 'naturalised' by APC and therefore native to Australia. The second subset, hereafter referred to as the 'naturalised' species, contained 237,541 records of 2,699 species considered 'naturalised' by APC and therefore 'alien' to Australia. The third subset, hereafter referred to as the 'first record of naturalisation' dataset, contained only the first herbarium record for each of the 2,699 naturalised species in Australia. Importantly, this dataset does not imply the exact date of introduction nor naturalisation (which are unknown), merely the date first recorded by herbaria. The first records dataset is analogous to those of Pyšek *et al.* (2003) and Sullivan *et al.* (2004).

(B) **Species composition and diversity**

Species composition was summarised by genus and family for both the native and naturalised datasets allowing comparison of their taxonomic composition. The ratio of naturalised species per family relative to the total number of [accepted] species per family worldwide (The Plant List, 2014) was calculated to determine whether any families were over-represented relative to their total size (*sensu* Pyšek, 1998). When determining family size, nomenclature followed The Plant List. Otherwise, species concepts (including higher taxonomic groupings) followed APC (CHAH, 2014a) [which follows APG III (Bremer *et al.*, 2009) for angiosperms and Mabberley (2008) for

gymnosperms]. The net and cumulative number of species, genera and families was calculated over 1, 5, 10, 15, 20 and 30 year steps up to the year 2010 (preventing issues caused by delays in record digitisation). Alpha diversity was estimated using the Shannon Index (Shannon, 1948) in the vegan package (Oksanen *et al.*, 2013).

The taxonomic uniqueness of the naturalised flora relative to the native flora was calculated for each cohort by measuring the change in the phylogenetic diversity over time. To do this, we built a phylogenetic tree for the complete Australian flora at the family scale based on the APG III mega-tree (Bremer *et al.*, 2009) using the Phylocom program (Webb *et al.*, 2008). We then aged the nodes of the tree using Phylocom's Branch Length Adjuster (BLADJ) algorithm based on the age records contained in Wikström *et al.* (2001). The tree was imported into R using the taxize (Chamberlain & Szocs, 2013) package where the phylogenetic diversity (PD) of the tree was estimated by calculating the sum of the branch-lengths joining the root node to the tips (Faith, 1992). The phylogenetic diversity in earlier time periods was calculated by sequentially removing the tips corresponding to families that naturalised in each time step using the ape package (Paradis *et al.*, 2004) and re-calculating Faith's PD.

Several analyses were also undertaken to explore the potential for underlying bias in the dataset due to differences in collection effort over time (*sensu* Aikio *et al.*, 2010; Lavoie *et al.*, 2012). The rate of new detections as a function of the total number of specimens collected per cohort was calculated, as was the overall ratio of alien to native specimens, the ratio of specimens to collection events and various additional combinations of these metrics. Considerable cross checking of the dataset

occurred at this step, ensuring that naturalisation status and taxonomy were reported correctly.

(B) **Geographic distribution and likely source origin**

The range of a species can be defined as either its endemic 'origin' or its more inclusive 'distribution' that includes locations where the species has naturalised outside its native range (Kloot, 1984). Because the aims of our analysis included identifying high-risk pathways, we used species' known 'distributions' to account for the possibility of species spreading from locations outside their native range. This differs from previous studies that draw continental scale 'origins' from Mabberley (2008).

The geographic distribution of a species was, therefore, determined by identifying the countries where it was known to occur prior to its discovery in Australia. To do this we used the *dismo* (Hijmans *et al.*, 2013) package to query the Global Biodiversity Information Facility (GBIF, 2014) for all georeferenced herbarium records of each species, including their synonyms, prior to that species' collection date in our first records dataset. That is, if a species was first found in Australia in 1900, the GBIF query only returned occurrences collected prior to 1900. Species were assigned multiple possible source origins where they were returned, capturing the broadest interpretation of relevant information.

Patterns in likely source distribution were identified by constructing contingency tables of the frequency of countries by time period and plant family. As with species composition, we used the Shannon Index to estimate alpha diversity. To visualise the data we mapped the number of links per country within 1, 10 and 30

year time steps. Maps were prepared using the ggplot2 (Wickham, 2009) graphics package with the sp (Pebesma & Bivand, 2005), rgdal (Bivand *et al.*, 2013) and rgeos (Bivand & Rundel, 2013) packages installed.

(B) **Economic use and introduction purpose**

Modes of species introduction are uncertain. Based on research that closely linked introduction purposes to predominately economic uses (Groves, 1998; Mack & Erneberg, 2002; Virtue *et al.*, 2004), we used the peer reviewed World Economic Plants (WEP) database (Wiersma & Leon, 2013; USDA, 2014) to infer the likely purpose of introduction into Australia. WEP classifies species' economic uses according to the Economic Botany Data Collection Standard (Cook, 1995) developed by the international Taxonomic Databases Working Group (TDWG). For each naturalised species, we queried WEP using a script that returned a list of economic uses for the species, or 'no listed use' where the species was not found, or had no known use. Where WEP recorded a species as a known 'weed' (anywhere in the world), this was also added to our dataset.

To ensure our economic uses were as comprehensive as possible, where a species had no listed use, we supplemented the WEP data with the Australian Government's *Catalogue of cultivated plants* (Ingram, 2009). The catalogue includes over 50,000 plant species known to have been deliberately cultivated in Australia and has previously been described in Phillips *et al.* (2010a) and Phillips *et al.* (2010b). Where a species had multiple economic uses (~20%) these were retained as the specific use resulting in naturalisation is typically unknown, however, highly-unlikely uses such as traditional poisons were removed. Similar to the analysis of patterns in geographic distribution, patterns in economic use were identified by constructing a

series of contingency tables including frequencies of economic category by time step and plant family.

(B) Pathways as the interaction between likely source, purpose and time

The interactions between geographic distribution (likely source), economic use (likely introduction purpose) and time were identified by constructing contingency tables of the frequency of each interaction occurring in the dataset compiled during the previous stages of the analysis. To visualise the data we prepared a bubble plot, similar to the approach of Zenni (2014). Due to the presence of zeros in the three way contingency table, we were unable to test the statistical significance of these patterns using a chi-square analysis, limiting the inferences we can draw from this analysis.

Unless otherwise specified, all analyses were undertaken in the R software environment (R Core Team, 2013) with the reshape2 (Wickham, 2007) and plyr (Wickham, 2011) data management packages. All plots were generated using the ggplot2 (Wickham, 2009) graphics package with the RColorBrewer (Neuwirth, 2011) package. The R script used for the analysis is included in the supplementary material, as are the scripts written to query the APC, TPL and WEP/GRIN websites (Supplementary Material S2-5).

(A) RESULTS

(B) Taxonomic composition

In total, 2699 naturalised species belonging to 1061 genera and 161 families were identified from the 3,074,544 valid catalogue records held by Australian herbaria (Table 1). This corresponded to a naturalised species density of 392 sp./log(km²) and a species to family ratio of seventeen. Using our 'native' dataset as a baseline for the number of native species (20,376 sp.), approximately 12% of the total flora of Australia (23,075 sp.) was naturalised. Of these species, 1993 (74%) were dicots, 660 (24%) were monocots, 32 (1%) were gymnosperms and 14 (1%) were pteridophytes (Table 1). The families Poaceae (339 sp.), Legumiosae (286 sp.) and Compositae (270 sp.) contributed 33% of the overall species total (Figure 1a). Forty-three families (27%) contributed only one species each (Supplementary Material S1). The genera *Trifolium* (38 sp.), *Solanum* (32 sp.), *Cyperus* (25 sp.), *Euphorbia* (25 sp.) *Erica* (24 sp.) and *Juncus* (24 sp.) were the most prevalent (Figure 1b). 612 genera (58%) contributed only one species each (data not shown).

The number of alien species per family was significantly correlated with the total number of species in the family world-wide, with the fit improving ($R^2=0.62$, $p=8e-11$) once the total was adjusted to remove native Australian species (therefore, unable to naturalise) (Figure 2). Whilst several families appeared to have high leverage, and were possibly significantly over- or under-represented relative to their size, a Bonferroni test (Fox & Weisberg, 2011) failed to detect any significant outliers (Bonferroni $p > 0.05$).

(B) Temporal changes in richness and diversity

Naturalised species richness increased linearly at a rate of approximately 20 species per year between 1880 and 2000 with an apparently lower rate either side of this time period (Figure 3). Similar patterns were observed at both the genus and family levels; adding approximately seven genera and one family per year over the same period (data not shown). At the family scale, this increase in species richness corresponded to an equivalent increase in total phylogenetic diversity of approximately 8% (Figure 3). However, in contrast to species richness, total phylogenetic diversity increased exponentially over time. The Shannon Index (H') (Shannon, 1948) of species within families also increased across ten year intervals from 2.5 in 1840-1850 to 3.75 in 1990-2000 (Figure 4), indicating that the naturalising species were more evenly distributed across a larger number of families in recent intervals.

When analysed in conjunction with collection effort (the total number of specimens collected in the cohort), the rate of return (new species detected per thousand specimens) was found to be declining with time (Figure 5). This pattern was present regardless of whether collection effort was measured as a function of all specimens or only alien specimens (data not shown); accounting for possible changes in the historical priority given to the collection of alien species. The ratio of native to alien specimens was found to be highly variable, fluctuating between 3-13% since 1900 (data not shown), with an overall rate of 8.6%.

(B) Geographic distribution and likely source origin

The areas of western and northern Europe were the most likely source of species naturalised in Australia (Figure 6). At the continental scale, Europe contributed 47.4%, North and Central America 22.1%, Africa 14.3%, South America 7.8%, Asia

6.3% and Oceania 2.1% of the total species links. Over time the number of possible source countries increased, whilst the contributions of individual countries became more even (Figure 7). Similar to the increase in family diversity (species within families) (Figure 4), geographic source diversity (species within countries) increased from 2.6 in 1840-1850 to 4.5 in 1990-2000 (Figure 8).

(B) Economic use and introduction purpose

Ornamental horticulture was the most frequent economic use, contributing up to 1,783 (66%) species, including over 350 species in each of the last four 30-year intervals (Figure 9). Uses such as animal and human foods were more likely during the late 1800s to early 1900s, before declining in relative importance. The number of species not found to have an economic use gradually increased in each time step and, with the exception of ornamentals, surpassed all other uses to become the second largest category (65 sp.) in the period 1980-2010. Conversely, the number of new species considered to be weeds peaked at over 300 species in the period 1890-1920 before declining sharply to less than 100 species between 1980-2010. The database classifies 1026 (~38%) of the 2699 species as weeds.

(B) Pathways as the interaction between likely source, purpose and time

By inferring species' naturalisation to a likely source (geographic distribution) and likely introduction purpose (economic use) across 30 year cohorts we were able to identify high-risk pathways of introduction. For example, we were able to identify that ornamentals originate most frequently in the United States and that the frequency of this pathway is increasing across North America (Figure 10). Similarly, whilst the overall frequency of 'weed' species naturalising is declining, the number with known distributions in New Zealand is increasing.

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345 The temporal analysis also reveals the declining influence of Europe. With
346 the exception of Spain, the frequency of linkages across all use categories is either
347 steady or declining (Figure 10). Given that the overall rate of naturalisation has
348 remained constant (Figure 3), this has corresponded to a rise in the number of
349 species with linkages to the Americas and Asia. These changing dynamics are
350 reflected in the most likely naturalisations; between 1860-1890 a naturalised species
351 was most likely to be a Leguminosae or Poaceae species used for animal food from
352 France or Italy; by 1920-1950 the most likely species was a Poaceae used for animal
353 food from the United States or France; however, by 1980-2010 the most likely
354 naturalisation was an ornamental Iridaceae or Ericaceae species from South Africa
355 (Figure 10; data not shown).

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(A) **DISCUSSION**

Contrary to prevailing hypotheses (*sensu* Perrings *et al.*, 2005; Meyerson & Mooney, 2007; Hulme, 2009), we found no evidence that the annual rate of naturalisation has increased over time. Rather, species richness increased approximately linearly at a rate of 20 species per annum between 1880-2000. We found that the taxonomic diversity of newly naturalized species has increased, at least partially, due to changing pathways of introduction.

(B) **Patterns in taxonomy, geographic distribution and economic use**

On the basis of both size (2699 sp.) and density (392 sp./log(km²)), the naturalised alien flora of Australia could be considered one of the most species rich alien flora in the world (see Vitousek *et al.*, 1997; Weber, 1997; Vilà *et al.*, 1999). Our estimate of 2,699 species is slightly lower than the 2,739 species listed by Randall (2007). However, this small difference is almost certainly due to our narrower interpretation of the data to only include species with georeferenced herbarium specimens (see Randall, 2006) and the implicit limitation that those specimens need to be physically collected. The percentage of alien species within the total flora (~12%) is higher than other continental areas, but lower than many islands [including New Zealand] (see Vitousek *et al.*, 1997), matching the 'island continent' biogeography of Australia (Pyšek & Richardson, 2006).

The taxonomic composition of the Australian alien flora is similar to other large alien flora (Duncan & Williams, 2002; Lambdon *et al.*, 2008; Jiang *et al.*, 2011) with the three mega-families (Poaceae, Leguminosae and Compositae) contributing most (Figure 1a). Like Weber (1997) and Jiang *et al.* (2011), we identified a significant positive correlation between the number of species within a family that

naturalised and the total number of species within the family world-wide (Figure 2). We were unable to find evidence that any family was significantly over- or under-represented relative to family size. When we overlay the twenty most naturalised plant families world-wide identified by Pyšek (1998), thirteen have contributed more species to Australia than expected given their size (Figure 2), with the variation attributable to the previously demonstrated differences in their respective introduction pressure (Diez *et al.*, 2009; Hulme, 2012).

Western and northern Europe dominate the species' geographic distributions (Figure 6), particularly in the cohort of species that naturalised prior to 1900 (Figure 7). This is expected following the extensive efforts of 'acclimatisation societies' in the late-1800s to make Australia more reminiscent of western Europe (Whitehead, 2007). Within continents, countries with Mediterranean and temperate regions that matched the predominant climate of Australia were also frequent sources (Figure 7). The contribution of central and southern America was larger than in the previous analyses of the south-eastern Australian flora (Specht, 1972; Kloot, 1987c), reflecting the inclusion of tropical northern and western Australia in our analysis. This mirrors the high frequency of South American species found to have naturalised in adjacent areas of tropical Asia (Wu *et al.*, 2004; Jiang *et al.*, 2011; Khuroo *et al.*, 2012).

Like previous analyses (Groves, 1998; Virtue *et al.*, 2004), we found ornamental horticulture to be the most important category, contributing about 65% of the naturalised species richness (Figure 9). The substantial deliberate introduction of pasture species into northern Australia (Lonsdale, 1994; Cook & Dias, 2006; van Klinken *et al.*, 2015) was also evident through the ongoing naturalisation of species used for animal foods (Figure 9). The propagule pressure associated with these

deliberate introductions has likely contributed to the very large number of Poaceae (Figure 1a) in early cohorts.

(B) **Temporal changes in richness and diversity**

The linear increase in the number of naturalised species is not entirely unexpected as Specht (1981) also identified a linear trend for several states within Australia in his analysis of partial state census data. We speculate that, for Australia at least, the analyses implying exponential rates of increase (Carr, 1993; Groves, 1998) have arisen due to the use of census dates rather than collection dates when plotting the number of naturalised species. The availability of collection dates in AVH also allows us to check that the naturalisation rate is not being influenced by temporal changes in collection effort (*sensu* Aikio *et al.*, 2010; Hulme, 2012; Lavoie *et al.*, 2012).

The rate of new naturalisations detected per thousand specimens is inversely correlated with total specimens collected (Figure 5). This trend remains the same regardless of whether native or alien specimens are used as the denominator. This may imply that the recorded rate of naturalisation has accurately reflected the real rate of naturalisation, despite fluctuating collection effort and priority given to the collection of alien species. However, the number of specimens recorded does drop off sharply in the years after 2010, and for this reason, we have not emphasised the apparent slowing of the naturalisation rate in the final cohort of Figure 3 (2000-2010); we hypothesise that it is most likely an artefact of the delay between the collection and subsequent cataloguing of specimens (Stajsic & Vaughan, 2007).

Analysed at ten year intervals, the alpha diversity of families increased over time (Figure 4), although the number of species in an interval remained constant

(~200 sp.). The effect of this increased diversity can be seen in the large proportion of families (27%) that contribute only one species (Supplementary Material S1) and the exponential increase in total phylogenetic diversity at the family scale (Figure 3). This approach is quite rudimentary by phylogenetic standards, and as such, we have chosen not to overly emphasise its rate of increase. Nevertheless, the sustained increase in novel families arriving in Australia, demonstrated by the fact that Australia now has alien species from over 30% (Table 1) of all vascular plant families (The Plant List, 2014), is clear.

Similarly, the geographic source distribution of species has changed over time. As mentioned earlier, in the period prior to 1900, sources were almost exclusively confined to countries along the historic shipping routes from western Europe to Australia (Figure 7a). Because of the likely gaps in GBIF collections during these early years of the analysis the number and frequency of linked countries should be considered a lower bound, however, as the diversity of trade and transit has increased, so too has the alpha diversity of geographic source distributions (Figure 8). Therefore, whilst the rate of naturalisation has not increased concurrently with globalisation, the diversity of naturalised species has.

Patterns in alien species taxonomy and origin are strongly biased by the deliberate introduction of species (Pyšek, 1998; Lonsdale, 1999; Mack & Erneberg, 2002). By classifying species according to their purpose of introduction we are able to separate out the characteristics of species that were, at least nominally, introduced for a particular purpose. For example, understanding that the United States (US) is the most likely source distribution for ornamental species (i.e., deliberate introductions) allows managers to consider US horticultural trends when

determining general prevention priorities (Zenni, 2014). At an even finer level, understanding that South African Ericaceae and Iridaceae with ornamental value are the most frequent pathway in the current cohort can directly inform pre-border regulation.

(B) **Implications for management agencies**

The key benefit of our approach is being able to visualise how individual pathways have changed in their relative importance over time. In particular, we see that the individual components making up the 'average invader' (an ornamental Poaceae species from Europe) peak in importance at different time steps (Figures 6, 9 & 10). By concurrently analysing the data within cohorts, the transition from food species originating in Europe, through food species and ornamentals originating in North America, to ornamental and accidental species originating in South Africa (but also the Americas and Asia) becomes clear (Figure 10). These patterns are intuitive, given the socio-economic development of Australia, and their identification assists managers to forecast and plan to prevent potential future naturalisations.

One such example is that whilst deliberate introductions are well known to be important (Kloot, 1987a; Mack & Erneberg, 2002; Virtue *et al.*, 2004; Zenni, 2014), the proportion of species 'accidentally' introduced is increasing in both the US (Lehan *et al.*, 2013) and Europe (Hulme *et al.*, 2008). Because the majority of deliberately introduced species arrive via legal importation (Virtue *et al.*, 2004; Cook & Dias, 2006), our similar finding (Figure 9) may imply that border control measures, such as import risk assessment (see Pheloung *et al.*, 1999), are becoming more effective at preventing the legal introduction of 'invasive' species. Regardless, the number of known new 'weed' species naturalising in Australia has steadily declined since the

period 1890-1920 (Figure 9), similar to the findings of both Murray and Phillips (2012) and van Klinken *et al.* (2015).

In contrast, Cadotte *et al.* (2009) hypothesise that ornamental species are phylogenetically clustered due to their non-random (deliberate) selection. Given the increasing diversity of species arriving by accident (Figures 5 & 9), it follows that the increase in taxonomic diversity (Figure 3) may be driven by accidental introductions. Darwin's Naturalisation Hypothesis (see Daehler, 2001; Procheş *et al.*, 2008; Thuiller *et al.*, 2010) suggests less related species are more likely to become invasive. Whilst the evidence remains equivocal (Strauss *et al.*, 2006; Procheş *et al.*, 2008; Cadotte *et al.*, 2009; Thuiller *et al.*, 2010), this may explain why accidentally introduced species have a higher likelihood of becoming invasive (Virtue *et al.*, 2004; Phillips *et al.*, 2010a). Given this increase is relatively recent, these species likely constitute an under-rated risk (Pyšek *et al.*, 2011).

The prevention of accidental introductions is also more complex than the management of deliberate modes (Perrings *et al.*, 2005; Hulme, 2009) and this presents an exciting area of research. By using georeferenced herbarium records as the basis for our analysis, we may be able to identify hot-spots of naturalisation (see Hulme, 2009) and we have commenced such an analysis. We also expect that finer-scale analyses within Australia may better link pathways to biogeographic zones and other local factors. However, declining lodgement of herbarium specimens (Lavoie *et al.*, 2012) and diminishing interest in traditional taxonomy threatens to hinder future progress in the discipline (Pyšek *et al.*, 2013). While global connection improves exchange of taxonomic information, it would be unfortunate if that information were no longer collected.

514 (A) **ACKNOWLEDGEMENTS**

515 The authors would like to acknowledge David Cantrill, Rieks van Klinken, Gabrielle
516 Vivian-Smith, Richard Duncan and three anonymous reviewers for their helpful
517 comments on earlier versions of this manuscript. Alison Vaughan, Niels Klazenga
518 and Anna Monro helped us understand the nuances of AVH & APC. Robert Hijmans
519 generously expanded the functionality of dismo. Cam Webb and Steve Kembel
520 provided solutions for managing very-large trees in Phylocom. The Australian
521 Department of Agriculture provided access to the catalogue of cultivated plants.
522 John Baumgartner and Bill Dixon assisted coding the R script. This research was
523 supported by an Australian Research Council (ARC) Future Fellowship to M.M. and
524 the ARC Centre of Excellence for Environmental Decisions.

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817 (A) **SUPPORTING INFORMATION**

818 Additional Supporting Information may be found in the online version of this article:

819 **Appendix S1** Data table of key family level metrics

820 **Appendix S2** R script for the core analysis.

821 **Appendix S3** R script for interfacing with the Australian Plant Census (ANBG)

822 **Appendix S4** R script for interfacing with The Plant List (RBG Kew).

823 **Appendix S5** R script for interfacing with the Germplasm Resources Information

824 Network (USDA-GRIN).

825

826 (A) **BIOSKETCH**

827 **Aaron Dodd** is a biosecurity policy analyst with a particular interest in the
828 development of quantitative decision support tools. He works across the
829 management spectrum from on-ground managers through to applied researchers
830 and policy makers, capturing the unique insights that each discipline brings to
831 biosecurity.

832

833 Author contributions: A.D, N.A, M.B and M.M conceived the ideas; A.D collected the
834 data; A.D analysed the data; and A.D led the writing

835

836 **Table 1:** Summary of naturalised alien plant species, genera and families by higher
837 taxonomic group within the naturalised alien flora of Australia.

	Species	Genera	Families
Pteridophytes - Ferns and Allies	14	10	8
Gymnosperms – Cycads and Conifers	32	10	3
Angiosperms – Monocotyledons	660	226	30
Angiosperms – Dicotyledons	1993	815	120
TOTAL	2699	1061	161

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840 **Figure 1:** Twenty most common families (a) and genera (b) within the naturalised
 841 alien flora of Australia. Classification of families follows APG III (Bremer *et al.*,
 842 2009).

846 **Figure 2:** Comparison of the number of naturalised alien species within a family as a
 847 function of the total number of species in the family world-wide. The world-wide
 848 total was adjusted down to account for the native flora of Australia. The solid line is
 849 the regression slope fitted to the data ($R^2 = 0.62$, $p = 8e-11$) and the dashed line is
 850 the equivalent slope fitted by (Weber, 1997) for the naturalised alien flora of Europe.
 851 Triangles indicate that a family is also one the 20 most successfully naturalised
 852 families world-wide as identified by Pyšek (1998).

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Figure 3: Cumulative change in the species richness (solid line) and phylogenetic diversity (dashed line) of naturalised alien plant species in Australia for the period 1840 – 2010. Points shown are in ten year intervals. Diversity was estimated by Faith's PD (Faith, 1992); the sum of the branch-lengths joining the root node to the tips at the family scale.

862 **Figure 4:** Familial diversity (the alpha diversity of species belonging to families)
 863 within ten year cohorts of the naturalised alien flora of Australia for the period 1840
 864 – 2010. Diversity was estimated using the Shannon Index (Shannon, 1948). Points
 865 shown are ten year intervals.

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868 **Figure 5:** Number of specimens collected and catalogued within Australia's Virtual
 869 Herbarium within ten year cohorts (columns) for the period 1840 – 2010. The line
 870 indicates the rate of new species (Figure 3) found per thousand specimens collected
 871 in each time period. Points shown are the corresponding ten year intervals.

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875 **Figure 6:** Relative contribution of geographic source distributions within the
 876 naturalised alien flora of Australia, broken down by World Bank Economic Regions
 877 (cells) and continents (shading). Continental contributions were: Europe 47.4%, the
 878 Americas 29.9%, Africa 14.3%, Asia 6.3% and Oceania 2.1% of the total naturalised
 879 species richness.

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882 **Figure 7:** Count of geographic source distributions for species naturalising within 30
 883 year cohorts. Three periods are shown: 1830-1860 (a), 1890-1920 (b) and 1950-
 884 1980 (c) each are separated by 30 years. Map projection is Mollweide.

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888 **Figure 8:** Geographic source diversity (the alpha diversity of species belonging to
 889 countries) within ten year cohorts of the naturalised alien flora of Australia for the
 890 period 1840 – 2010. Diversity was estimated using the Shannon Index (Shannon,
 891 1948). Points shown are ten year intervals.

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895 **Figure 9:** Sum of known economic uses for species within 30 year cohorts of the
 896 naturalised alien flora of Australia for the period 1800 – 2010. Economic uses are
 897 classified according to the Economic Botany Data Collection Standard (Cook, 1995).
 898 The eight most common uses are shown (solid lines), along with the number of
 899 species classified as 'no listed use' or 'weeds' (dashed lines).

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Figure 10: Frequency of interactions between the economic uses (Cook, 1995) and geographic distribution of the naturalised alien flora of Australia broken into 30 year cohorts. The top 50 countries and eight economic uses are shown, ordered by longitude. Bubble size represents the frequency of the interaction. The labels for the economic uses are as follows: Adit – food additives; Eros – erosion control; Fodd – animal fodder; Forg – animal forage; HumF – human food; None – no listed use; Orn – ornamental; Soil – soil improver; Weed and Wood – wood.